

# Life history and population size variability in a relict plant. Different routes towards long-term persistence

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## ABSTRACT

A central tenet of conservation biology is that population size affects the persistence of populations. However, many narrow endemic species combine small population ranges and sizes with long persistence, thereby challenging this tenet. I examined the performance of three different-sized populations of *Petrocoptis pseudoviscosa* (Caryophyllaceae), a palaeoendemic rupicolous herb distributed along a small valley in the Spanish Pyrenees. Reproductive and demographic parameters were recorded over 6 years, and deterministic and stochastic matrix models were constructed to explore population dynamics and extinction risk. Populations differed greatly in structure, fecundity, recruitment, survival rate, and life span. Strong differentiation in life-history parameters and their temporal variability resulted in differential population vulnerability under current conditions and simulated global changes such as habitat fragmentation or higher climatic fluctuations. This study provides insights into the capacity of narrow endemics to survive both at extreme environmental conditions and at small population sizes. When dealing with species conservation, the population size–extinction risk relationship may be too simplistic for ancient, ecologically restricted organisms, and some knowledge of life history may be most important to assess their future.

## Keywords

Endangered species, life span, LTRE analysis, matrix models, population dynamics, PVA.

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## INTRODUCTION

It is widely acknowledged that population persistence greatly depends on population size and temporal fluctuations (Tuljapourkar & Orzack, 1980; Menges, 1992; Lande, 1993; Matthies *et al.*, 2004; Boyce *et al.*, 2006). The strength of the population size–extinction risk relationship, however, appears to differ considerably across species. For example, there are many relict and endemic taxa that combine small population sizes with long historical persistence, contradicting the theoretical prediction (Cowling *et al.*, 1996; Lavergne *et al.*, 2005; Petit *et al.*, 2005). Most likely, species life-history traits are key determinants of population resilience or vulnerability (Keith, 1998; Eriksson, 2000; García & Zamora, 2003; Jongejans & Kroon, 2005). Moreover, persistence is not species specific, and important among-population differences in demographic traits or population dynamics are common (Oostermeijer *et al.*, 1996; Menges & Dolan, 1998; Quintana-Ascencio *et al.*, 2003; Morris & Doak, 2005; Brook *et al.*, 2006). Since life-history traits vary among species and among populations within species, it is likely that the importance of population size for population persistence varies,

and that not all small populations are equal from a conservation point of view.

Palaeoendemic taxa with highly localized ranges are predominantly found in regions where past climate changes have not resulted in major extinction events (Thompson, 2005). In the Mediterranean basin, many are confined to harsh environments like rocky outcrops (Médail & Verlaque, 1997), and their ranges and population sizes are typically constrained by the patchy distribution of suitable habitat and their low colonization capacity. These rupicolous endemics are often classified as threatened because of their small spatial extent, despite the fact that very few population viability analyses have been conducted on such species to assess their actual dynamics and performance (Picó & Riba, 2002; García, 2003). Furthermore, little is known about the life-history and functional traits linked to their success for local persistence in this particular habitat (García & Zamora, 2003; Lavergne *et al.*, 2004).

In this study I examine the vital rates, population growth, and viability of the narrow endemic *Petrocoptis pseudoviscosa* Fdez. Casas (Caryophyllaceae). This is a palaeorelict species included as ‘vulnerable’ in the Spanish National Red List. It occurs in just

**Table 1** General information on the populations of *Petrocoptis pseudoviscosa* studied.

Population (years)	Total occupancy area (m <sup>2</sup> )	Estimated number of individuals (patch)	N monitored (% total)	% Reproductives* (SD)	% Seedlings* (SD)
Fch (95–00)	10	130	118 (91%)	13.3 (4.8)	9.7 (5.4)
Abi (95–00)	2500	1500 (850)	152 (18%)	59.9 (5.5)	5.6 (3.4)
V (96–00)	1,500,000	45,000 (1500)	454 (1%)	35.4 (4.3)	18.8 (5.4)

\*Mean values over years, and standard deviation.

one small valley of the Spanish Pyrenees, where five populations of very different size (130–45,000 individuals) exist. Populations are at distances of 2–6 km from each other, and spread over a total area of 22 km<sup>2</sup> (García *et al.*, 2002). The species is restricted to bare rocky walls and overhangs that are patchily distributed across an abrupt topography, and the isolation of populations is reinforced by the species' seed-dispersal system that strongly reduces the probability of long-distance settlement (see below). The overall situation is comparable to many other endemics growing in mountain ranges of the Mediterranean Basin (Thompson, 2005).

This study has the following particular aims: (1) to assess the spatio-temporal variability of reproductive and survival parameters in three adjacent populations of dramatically different sizes; (2) to model how vital rates translate into population growth rates, and examine the life-history components that most contributed to such spatio-temporal variability in population dynamics; and (3) to assess the long-term vulnerability, by exploring the relative importance of life history and population size.

## METHODS

### The species and populations monitored

*Petrocoptis pseudoviscosa* Fdez. Casas (Caryophyllaceae) is a perennial herb that grows exclusively in crevices of calcareous rocky vertical and overhanging walls. The white flowers, produced on elongated inflorescences, are mainly pollinated by hoverflies (pers. obs.). Fruit capsules contain about five seeds with a tuft of hairs becoming slightly sticky when wet. Inflorescence stems move towards the rock during fruit maturation; seeds are released close to the wall and can establish if delivered to a humid or muddy crevice. Establishment usually occurs in the direct vicinity of the mother plant, although the occurrence of isolated seedlings suggest that there is some secondary seed dispersal. Plants do not reproduce vegetatively.

The study was conducted in the Esera Valley (Spanish Pyrenees). Three of the five extant populations were monitored: Fuente del Churro, Abi, and Ventamillo (hereafter Fch, A, and V). These three populations are the only ones with a sufficient number of plants available to allow a detailed demographic study. They span the species' whole geographical (UTM 31TBH89/80/90, respectively) and altitudinal (Fch: 700, V: 850–1050, A: 1200 m a.s.l.) distribution, as well as the range of

population sizes (see Table 1). Given its small area of occupancy, population Fch could be followed almost completely, while only accessible plants were monitored in the others. Population A consists of two patches (less than 200 m away) of similar size, and only one of them was monitored. Population V consists of several patches scattered over a few hundred metres following the river valley; one patch was monitored here. In this case, and due to the inaccessibility of most plants, it is impossible to test if the vital rates recorded are representative of the population ones. Nevertheless, many of the patches are located in similar places to the one monitored: shadowy walls of a deep river valley.

Plant density in rocky walls is totally determined by crevice availability, it seems to be similar in all populations, and probably not far from the carrying capacity (pers. obs. and unpublished data from hand-sowing experiments). The well-delimited patchy spatial distribution, the distances between all known populations (2–6 km straight line, but much longer for pollinators due to the strong relief of the area), and the antitelechory system suggest that gene flow between populations is either inexistent or very low.

### Sampling data and matrix parameterization

In order to explore the spatio-temporal variability of reproductive and demographic parameters, each accessible individual was mapped in spring 1995 (1996 in population V), numbered, and followed through 2000. In July of each year, I recorded the number of rosettes for all plants and the flower and fruit number for fertile individuals (non-fruiting flowers stay on the plant until late summer). Seedlings emerged within the monitoring areas were searched yearly, mapped, and included in the monitoring. Flower and fruit predation was also recorded each year. Altogether, 724 individuals were followed during the 6 years of study.

The life cycle of the species was broken into six classes, with plants classified according to both stage and size-based criteria. There are three very well-defined classes: seeds (sd), first-year seedlings (with visible cotyledons; sdl), and juveniles (one shoot, mainly non-reproductive plants; juv). Three more classes of adult plants were differentiated according to the number of shoots: small (2–5; sm), medium (6–9; md), and large ( $\geq 10$ ; lg), in order to achieve roughly similar numbers of individuals per class. Demographic fates of monitored individuals were computed as probabilities of transition to any class, separately for each year and population.

Seed production was estimated for the transition matrix as the product of (i) the recorded number of non-preyed fruits, and (ii) the mean number of seeds per fruit. A factor accounting for the probability of being sowed in crevices was included in the probability of a seed in the mother plant to enter the seed bank or germinate within the next year. That factor takes into account the ratio of seedlings:seeds over the study period, as well as the germination rate, which are specific for each population. Germination rates in the years after seed release were estimated from repeated hand-sowings over consecutive years in a total of 61 crevices (Fch: 2, A: 26, V: 33). Twenty-five seeds were gently introduced per crevice, and their fate followed for 2–5 years (germination rate was so low in population A that 50 seeds were used instead for hand-sowings from 1998). Due to the difficulty of carrying out extensive hand-sowings under field conditions and the low germination rates, I used pooled population values for germination rates over years. Although seeds were recorded to germinate up to the third year within crevices, none germinated after 10 years in a green house. For this reason I fixed yearly dormancy in the seed bank to 0.5 (meaning that the probability of dying is also 0.5 every year, and that the probability of germination in 10 years would be as low as 0.1%).

### Matrix analysis. General performance

Matrix models were used to explore population dynamics, important life-history components, and past and future performance. Fourteen yearly projection matrices (Fch = 5, A = 5, V = 4) were constructed from estimates of reproduction, seed fates, and transition probabilities among stage classes. They were the basis for linear time-invariant matrix models of the form  $n_{t+1} = A * n_t$  (Caswell, 2001), where  $n_{t+1}$  is a vector with the abundances of stages in the population at time  $t$ , and  $A$  integrates all the probabilities ( $a_{ij}$ ) for an average individual plant in class  $j$  at a moment  $t$ , to be in class  $i$  after 1 year. The dominant eigenvalue ( $\lambda$ ) of the projection matrix, or population growth rate associated to each matrix, characterizes the deterministic properties at a particular site and time. To construct 95% confidence intervals (CI) for the projected population growth rates, bootstrap resampling was applied to the observed fates of monitored plants for each year and population. The CI was obtained from the distribution of  $\lambda$ -values generated from 3000 bootstrapped matrices constructed from random draws of individuals. The bias-corrected percentile interval method provided the lower and upper bounds (see Caswell, 2001). The overall population growth rate over the study period was computed from the real sequence of  $n$  correlative matrices recorded, as the  $n^{\text{th}}$  root of the highest eigenvalue of the resulting matrix for each temporal series ( $A_n * A_{n-1} * \dots * A_1$ ).

Temporal variation in population growth rates was computed as the variance of ( $N_{t+1}/N_t$ ) over 10,000 iterations after discarding the first 1000 values to eliminate transient effects. An initial population vector representing the current frequency of individuals at each patch was used to project population growth rate over successive time intervals, using a matrix drawn at random for each interaction.

The associated right eigenvector of a matrix ( $w$ ) corresponds to the stable stage distribution projected by a deterministic model. One way to explore the consistence of past and present demographic rates is to compare actual and predicted stage distributions (Doak & Morris, 1999). To do so, I calculated the stable stage structure from the average matrix for each population, and compared it with the average numbers of each class, excluding seeds, over the study period.

Life span was estimated using the algorithm reported in Cochran & Ellner (1992) as the maximum value of 'conditional total life span', or mean age at death conditional on reaching a given stage (the largest class in this case), minus one. For each population, life span was calculated as the harmonic mean of the life spans from each yearly matrix (Ehrlén & Lehtilä, 2002). Given the strong dependence of life span on mortality rates, which in turn determines the population growth rates, this estimate of longevity can be affected by the increasing or decreasing trend provided by each matrix. To minimize this bias, I recalculated life span only from matrices whose  $\lambda$  did not differ significantly from one.

### Matrix analysis. LTRE

A retrospective analysis was performed in order to estimate the contribution of different life-history traits on the observed temporal and spatial  $\lambda$  variability (Life Table Response Experiments, thereafter LTRE; Horvitz *et al.*, 1997). Population and year were included as fixed factors, considering that the three populations were selected because of their particular size (representing a gradient of the species range), and years as a period representative of the current environmental conditions. The main effect of population and year, and their interaction, was computed according to the following two-way model:

$$\lambda^{(py)} = \lambda^{(-)} + \alpha^p + \beta^y + (\alpha\beta)^{(py)}$$

where  $\lambda^{(-)}$  is the growth rate calculated from  $A^{(-)}$ , the overall mean matrix of all matrices included in the analysis,  $\lambda^{(py)}$  corresponds to each yearly matrix, and  $\alpha^p$ ,  $\beta^y$ , and  $(\alpha\beta)^{(py)}$  are the population, year, and interaction effects (the year 1995 was excluded, because no data were available for population V). These effects can be decomposed into contributions from each matrix element (deviance to the corresponding element of the mean matrix) times its sensitivity evaluated at the midpoint of the matrices being compared. Thus, the decomposition analysis gives the positive or negative contribution of each matrix entry to each effect (population and year) and their interaction (population by year). For a detailed description of the method see Horvitz *et al.* (1997). In order to get a clearer biological picture of contributions, besides computing the overall total effect (i.e. the sum of absolute values), and net effect (i.e. the sum of positive and negative values) of population and year, I summed the positive and negative LTRE contributions for each life-history component separately: fecundity (F), stasis (S), growth (G), and retrogression (R). This dissecting procedure allows to explore how positive and negative contributions compensate each other and to show

hidden trade-offs between life-history components (Jongejans & de Kroon, 2005).

### Matrix analysis. Future viability

To compare population trends in the long term, the stochastic growth rate ( $\lambda_s$ ) and an approximated 95% confidence interval were calculated by simulation (stoc\_log\_lam routine provided by Morris & Doak, 2002). The population growth was projected over 50,000 time intervals, using a matrix drawn at random each time. The log ratios of the initial and final population vector after each interval ( $N_{t+1}/N_t$ ) were used to compute the mean and variance of population growth increments.

The vulnerability of this species in the next century was also estimated by simulation, as the probability of extinction ( $< 1$  individual left) of each natural unit monitored (current patch sizes and structures were used; no seeds included in the initial vector). The 'simex' routine of Morris & Doak (2002) was used, based on random selection of annual matrices (independently and identically distributed environmental conditions) and assuming no demographic stochasticity. Due to the strong spatial variability found for population size and life-history traits, I explored the relative importance of population size on future persistence; in particular, if small populations would have the same chance at each place. To do that, I compared the probability of extinction for theoretical patches of  $N = 100$  plants, controlling for the particular proportion of classes and environmental stochasticity of each population. Neither this nor the former analyses have any predictive value; they are used to compare the vulnerability of each patch in relative terms. All described analyses were conducted with the software MATLAB version 6.5.

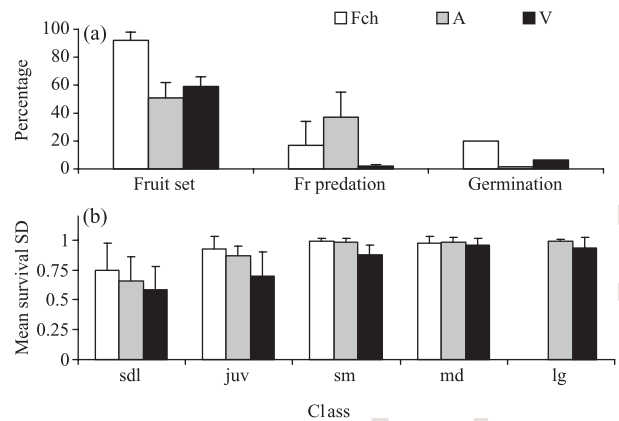
### Statistical analysis

Stasis was the transition with highest probability and elasticity values, being the most important drivers of the population dynamic system. Log-linear models were first used to test if survival rates of the largest class differed among populations (stasis vs. death or retrogression), so that differences in the probabilities of these matrix elements were not generated by chance. The frequency of plants in each class or state was compared among populations or models (current vs. expected) using chi-squared tests. A nominal logistic test was used to compare seedling performance of different cohorts among populations.

## RESULTS

### Spatial variability of reproductive and survival parameters

The overall composition of populations differed significantly when considering the frequency of seedlings, vegetative, and reproductive individuals ( $\chi^2 = 42.29$ , d.f. = 4,  $P < 0.0001$ ; Table 1). All populations had low recruitment, as the proportion of seedling ranged from 10% to 19%. Surprisingly, however, the



**Figure 1** Spatio-temporal variability of (a) parameters linked to population recruitment over 6 years (mean + SD): ratio of fruits/flowers produced (fruit set as percentage), fruit predation (Fr predation), and germination rate (% for all hand-sowings carried out over 3 years pooled), and (b) annual survival probability (mean + SD) for each class at each population (sdl: seedlings, juv: juveniles, sm: small adults, md: intermediate adults, lg: large adults).

population with consistently highest proportion of seedlings (V) was not the one with highest scores in parameters related to fecundity like frequency of flowering plants (Table 1), number of flowers per plant (from  $33 \pm 46$  in A to  $6.3 \pm 9.6$  in Fch), fruit set, or germination rate (Fig. 1a).

Seedling survival differed likewise among populations (nominal logistic model,  $\chi^2 = 33.64$ , d.f. = 11,  $P = 0.0004$ ,  $n = 304$ , 4 cohorts used: 1996–99), and the significant effect of the likelihood ratio test for the interaction pop \* year ( $P = 0.0015$ ) indicates that any given year may be better or worse for seedling performance depending on the population. Seedling growth rates also varied considerably among populations: during the first year, they grew only up to juveniles in the Fch population, while some seedlings started to flower and developed up to four rosettes in the other two populations. Survival of reproductive plants was very high and nearly constant across years (Fig. 1b). Population V showed the lowest and population A the highest survival rates, for all classes. This resulted in marked among-population differences in life span, with plants dying from an average age of 18.4 years in V to 50 years in A. Among-population differences in survival of the highest class were significant ( $P < 0.0001$  always), meaning that the probabilities for stasis used in the matrices are really different and not just a matter of the sample size.

### Population growth rates, and the relative importance of life-history components

Deterministic annual lambdas projected growth tendencies that ranged from  $-22.7\%$  in population V to  $+9.1\%$  in Fch. Eight out of 14 significantly differed from one (Fig. 2). Population lambdas over the study period, however, were closer to the equilibrium: from  $-3.14\%$  to  $+0.87$  (see Table 2). Overall, population A was the most stable, as its yearly lambdas were closest to unity and least variable over time (Table 2).

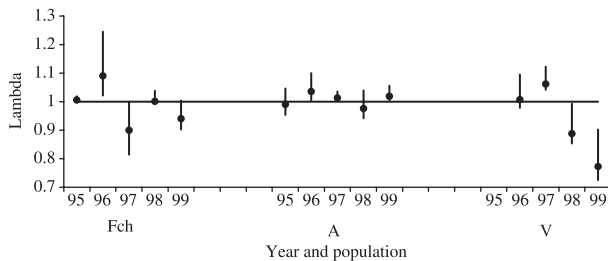


**Table 2** Population dynamics and life span for the three populations of *Petrocoptis pseudoviscosa* monitored over the 1995(6) to 2000 period.

Population	$\lambda$ <i>n</i> years*	Temporal variance†	Stochastic $\lambda$ (95% confidence Interval)
Fch	0.9938	0.0034	0.9906 (0.9899–0.9912)
Abi	1.0087	0.0004	1.0078 (1.0059–1.0098)
V	0.9686	0.0096	0.9478 (0.9469–0.9487)

\*Computed as the *n* root of the resulting product of yearly consecutive.

†Computed from stochastic growth (see text for further details).



**Figure 2** Population growth rates from deterministic models (Fch: Fuente churro, A: Abi, V: Ventamillo). Only the two last digits of each year's transition are shown (for example 95 corresponds to 1995–96). The error bars are bootstrapped 95% confidence intervals.

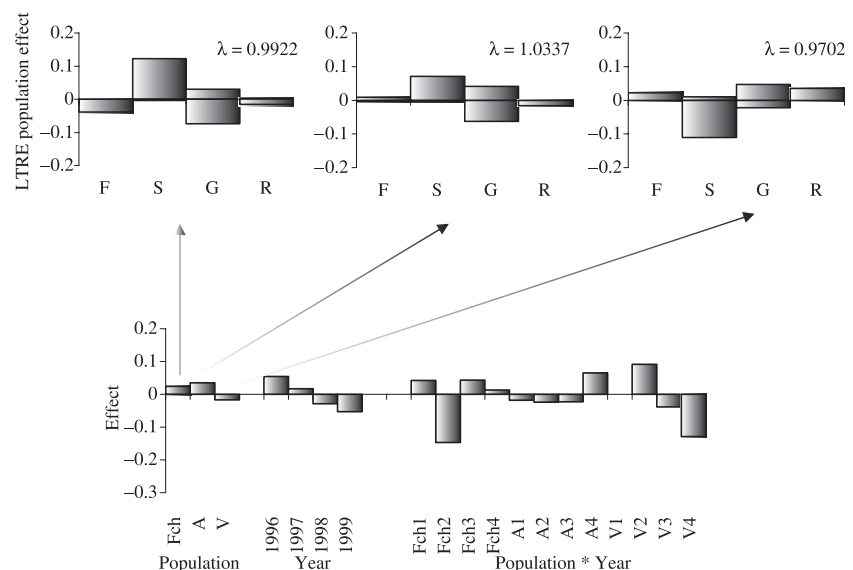
In order to explore which life-history traits were most responsible for the observed lambda variability, this was decomposed into population, year, and their interaction in a retrospective LTRE analyses. Focusing on the magnitude of the effects (absolute values summed), the population effect was highest (mean  $\pm$  s.d. of the 3 average population matrices:  $0.249 \pm 0.041$ ), followed by the interaction effect ( $0.183 \pm 0.05$ ;  $n = 12$ ) and the year effect ( $0.114 \pm 0.015$ ;  $n = 4$ ). Focusing on the direction of the net effect of the contributions (positive and negative values summed), however, the year effect was in general larger than the population effect (Fig. 3, lower diagram). These contrasting results for

the population effect indicate important within-population compensations between positive and negative contributions of life-history traits accounting for lambda variation.

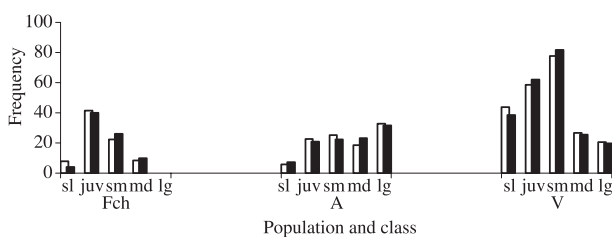
Stasis was the life-history component with the largest contribution to the population effect, being positive in populations Fch and A, and negative in V (Fig. 3, upper diagrams). A negative LTRE effect for stasis in the V population indicates that the relative low value for such life-history component is mostly responsible for the lower lambda value in that population relative to the overall. The positive effect of fecundity and growth in the same population was not enough to buffer the negative contribution of stasis. Growth and regression had a negative effect in the other two populations (Fch and A), but they were compensated by the positive effect of stasis. The magnitude and sign of the fecundity component varied among populations, but it consistently had a small role compared to other life-history components.

### Past and future trends

Current population structures are the result of past vital rates, while stable structures generated by deterministic models are the projected output of current vital rates. Despite the fact that the three populations exhibited totally different stage histograms according to the size model's classification ( $\chi^2 = 75.4$ , d.f. = 8,  $P < 0.0001$ ; average population frequencies in each class over the



**Figure 3** Lower diagram: Population (white bars), year (black bars), and population \* year (grey bars) effects in the variance decomposition of  $\lambda$  (LTRE fixed design) in *Petrocoptis pseudoviscosa*. For the population factor (upper diagrams), the positive and negative contributions of matrix elements are grouped by life-history components: fecundity (F), stasis (S), growth (G), and retrogression (R). The overall mean  $\lambda$  (all populations and years) is 0.9703, and mean population  $\lambda$ s over years are provided in each diagram.



**Figure 4** Average proportion of each class (from left to right within each population: seedlings, juveniles, small adults, intermediate adults, large adults) over the 5–6 years of monitoring at each population (white bars), and projected proportion (black bars) by deterministic models. None of the within population comparisons was significant (see text for more details).

study period were used to compare with projected frequencies), current and stable structures showed a remarkably similar pattern at each place ( $\chi^2 = 1.96, 0.79$  and  $0.71$  for Fch, A and V, respectively; d.f. = 3 for Fch and 4 for A and V;  $P > 0.58$  in all cases; Fig. 4).

The stochastic growth rate resulting from simulations was significantly increasing ( $\lambda_s > 1$ ) in the intermediate size population (A), and significantly decreasing ( $\lambda_s < 1$ ) in the smallest and the largest one (Fch and V, respectively; Table 2). Stochastic models projected no extinction risk within the next century for the small and intermediate populations (total number of plants:  $N = 130$  and  $850$ , respectively), and a 5.7% of probability for the studied patch of the largest population ( $N = 1500$ ). When patch sizes are all reduced by simulation to 100 plants to test the vulnerability of the species at different places (each with a particular set of life-history traits), the extinction probability would raise to 78% in population V, while no extinction events resulted in the other two simulated populations.

## DISCUSSION

### Spatial variability of life-history components

The three populations studied along a river valley do not show clear differences related to density, and are close enough as not to expect important macro-climatic differences either. Nevertheless, they likely have a different microclimate: the studied patch of the largest population (V) is distributed deeper in the valley, in shadow and humid rocks near the river, while the other ones are located in walls more exposed to sun and wind. Probably for this reason, recruitment is higher, plant growth is faster, and plants are larger in V (leaves are almost twice as long in V than in A; unpublished results). In addition, the longevity of established individuals, together with the difficulty for seed dispersal and the consequent founding of new populations in available empty rocky patches, suggest that the existing populations are old. Thus, despite the proximity of the three populations, strong local adaptations seem possible.

Populations become extinct if recruitment does not outweigh mortality of established plants for extended periods like the

generation time. For ancient organisms therefore the amount of seedling recruitment is expected to fit well the mortality schedule of plants locally adapted to each particular place. In this study, important among-population differences have been found for different rates linked to recruitment (flower production, fruit set, fruit predation, and germination), but none of them, taken alone, would have been able to predict the better or worse population dynamics. Actually, the most stable population with the highest stochastic population growth rate (A) only exceeds the other two in flower production, whereas it ranks worst for all other reproductive rates.

Strong differences in population structures were also observed at the local scale of this narrow endemism, which were best explained by differences in the growth rate of seedlings (probability of moving to larger classes), and the timing of adulthood. Again, the most stable and least vulnerable population from a demographic point of view (A) would have been ranked as the most senescent from a snapshot, because it contained the highest proportion of reproductive plants and lowest frequency of seedlings.

Taken together, these results suggest that using reproductive rates, recruitment, or the frequency of stage classes for comparing the success of populations under different management or vegetation succession at regional scale (Oostermeijer *et al.*, 1994; Brys *et al.*, 2003; Endels *et al.*, 2004), may not be equally useful for all species. The spatial variability recorded within the same small valley, and its low correlation with overall population performance, indicates that population structure need not always be a suitable indicator of population dynamics in long-lived plants (see also Johnson *et al.*, 1994; Bruna, 2003; García, 2003). This hints at the need for using more reliable and universal parameters to assess and compare population vulnerability.

### The keys for local persistence through time

Spatial variability in reproductive and demographic traits is common in species that occur across large geographical ranges, but striking for a narrow endemism strictly linked to a very specific habitat. In *Centaurea corymbosa*, a monocarpic mediterranean endemic rocky plant restricted to  $3 \text{ km}^2$ , Fréville *et al.* (2004) found that most of the spatio-temporal variability in  $\lambda$  was due to the fecundity component. Despite the important spatial variability of reproductive rates found in *P. pseudoviscosa*, survival was the component with highest contribution to spatial variance. The strong effect of the pop\*year interaction resulting from the LTRE analysis, also found for seedling survival, together with the difficulty for genetic flow, suggests that populations may be locally adapted and respond differentially to the same overall weather. Nevertheless, phenotypic plasticity could also account for part of the among-population differences resulting from slight microclimatic conditions. An interesting question is how life-history components assemble, both in time and in space, to result in different successful combinations that lead to local population persistence over historical periods, i.e. for populations of totally different sizes to maintain themselves in different ways.

The population with lowest survival rates for all classes was also the most fluctuating (V), but it had the highest recruitment rates. The high temporal stability and survival rates of the intermediate size population (A), on the other hand, seem to be the key factor to render it highly independent on recruitment and thus potentially less vulnerable from a demographic point of view. The small population (Fch) is expected to experience a higher demographic stochasticity. Besides, its reduced occupation area may increase environmental stochasticity because all individuals in this population are likely to react in a more similar way to macroclimatic variation than hundreds of them dispersed over an extended area like the large (V) population, where the different reaction of individuals experiencing various microclimatic conditions might buffer among year environmental variability. Theoretically, this would translate into higher vulnerability of the small population due to the stronger influence of stochastic events. Nevertheless, this population was closer to equilibrium and less fluctuating than the largest one during the study period. It showed the highest survival, fruit set, and germination rates, which seems to be enough to balance the slow growth of plants, and to avoid extinction risk for the next century under current conditions. In both the Fch and the V populations the stochastic population growth rate was estimated as significantly negative, however, the chances for extinction in the long term were very different, and thus also the possibility of recovering during favourable years. This small population is a good example on how the recalled negative effect of environmental and demographic stochasticity (fluctuating lambdas and small population size, respectively) might be relative because it will depend on how they are buffered by the particular life-history components of each organism at each place.

The remarkable similarity of current and predicted population stage distributions in this plant suggests that the demographic rates recorded over 6 years are not significantly different from the ones in the past decades (Doak & Morris, 1999). This remnant dynamics (Eriksson, 1996) is typical of long-lived organisms (the estimated life span of *P. pseudoviscosa*, 50 years old at the intermediate population, is above the average of herbaceous plants, Ehrlén & Lehtilä, 2002), and also common among plants that grow in harsh habitats such as bare rocks (Morris & Doak, 2002; García, 2003; Forbis & Doak, 2004). In these marginal habitats, there are scarce opportunities for recruitment and resources, and long-lived plants of slow growth seem to have been selected over historical periods (Larson *et al.*, 2000; Picó & Riba, 2002; García & Zamora, 2003; García, 2003; Hampe & Petit, 2005). This study provides some insights into the capacity of narrow endemics to survive both at extreme environmental conditions and at small population sizes.

Simulated demographic projections indicated that population viability is not clearly related to population size or spatial extent in the case of *P. pseudoviscosa*, and that within species life-history trait variability in time and space is a very important factor. I do not know to what extent this fact is widespread among plants, but it may have important implications for their management. Thus, not all populations are expected to respond in a similar way to events that would become more significant as a result of

ongoing global change, such as habitat reduction, population fragmentation, or climatic warming. Population size decrease would have worse consequences for patches of the largest population compared to the intermediate one. Likewise, an increase of environmental fluctuations or persistent droughts would be probably best buffered by the intermediate population, the one with highest survival rates, and the most independent on recruitment.

Small population sizes are often the consequence of recent habitat loss, but they are also the way of life for highly specialized organisms restricted to patchy and scarce habitats. This makes a big difference, as totally different ecological factors and selective forces have been operating in the past. In the first case we may be attending the fall or transient adjustment of the population, while the second one is probably a stationary situation. Thus, generalizations on the population size–extinction risk relationship may be too simplistic and should be used with caution, i.e. we have no clear idea of what the variance is around this relationship. Old endemic species with small populations may be more robust than thought as demonstrated in this study. Notwithstanding, the decline of these long-lived remnants may be very slow and difficult to be detected. In absence of the necessary long-term monitoring, our ability to assess the vulnerability of a population or plant species will be enhanced if important information like the past history, and the life span, is taken into account.

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## REFERENCES

- Boyce, M.S., Haridas, C. & Lee, C.T. (2006) Demography in an increasingly variable world. *Trends in Ecology & Evolution*, **21**, 141–148.
- Brook, B.W., Traill, L.W. & Bradshaw, C.J.A. (2006) Minimum viable population sizes and global extinction risk are unrelated. *Ecology Letters*, **9**, 375–382.
- Bruna, E.M. (2003) Are plant populations in fragmented habitats recruitment limited? tests with an amazonian herb. *Ecology*, **84**, 932–947.
- Brys, R., Jacquemyn, H., Endels, P., Hermy, M. & Blust, G. (2003) The relationship between reproductive success and demographic structure in remnant populations of *Primula veris*. *Acta Oecologica*, **24**, 247–253.

- Caswell, H. (2001) *Matrix population models: construction, analysis, and interpretation*. Sinauer Associates, Sunderland, Massachusetts.
- Cochran, M.E. & Ellner, S. (1992) Simple methods for calculating age-based life history parameters for stage-structured populations. *Ecological Monographs*, **62**, 345–364.
- Cowling, R.M., Rundel, P.W., Lamont, B.B., Arroyo, M.T.K. & Arianoutsou, M. (1996) Plant diversity in mediterranean-climate regions. *Trends in Ecology & Evolution*, **11**, 362–366.
- Doak, D.F. & Morris, W. (1999) Detecting population-level consequences of ongoing environmental change without long-term monitoring. *Ecology*, **80**, 1537–1551.
- Ehrlén, J. & Lehtilä, K. (2002) How perennial are perennial plants? *Oikos*, **98**, 308–322.
- Endels, P., Adriaens, D., Verheyen, K. & Hermy, M. (2004) Population structure and adult plant performance of forest herbs in three contrasting habitats. *Ecography*, **27**, 225–241.
- Eriksson, O. (1996) Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. *Oikos*, **77**, 248–258.
- Eriksson, O. (2000) Functional roles of remnant plant populations in communities and ecosystems. *Global Ecology and Biogeography*, **9**, 443–449.
- Forbis, T.A. & Doak, D.F. (2004) Seedling establishment and life history trade-offs in alpine plants. *American Journal of Botany*, **91**, 1147–1153.
- Fréville, H., Colas, B., Riba, M., Caswell, H., Mignot, A., Imbert, E. & Olivieri, I. (2004) Spatial and temporal demographic variability in the endemic plant species *Centaurea corymbosa* (Asteraceae). *Ecology*, **85**, 694–703.
- García, M.B. (2003) Demographic viability of a relict population of the critically endangered plant *Borderea chouardii*. *Conservation Biology*, **17**, 1672–1680.
- García, M.B., Guzmán, D. & Goñi, D. (2002) An evaluation of the status of five threatened plant species in the Pyrenees. *Biological Conservation*, **103**, 151–161.
- García, D. & Zamora, R. (2003) Persistence, multiple demographic strategies and conservation in long-lived Mediterranean plants. *Journal of Vegetation Science*, **14**, 921–926.
- Hampe, A. & Petit, R. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.
- Horvitz, C., Schemske, D.W. & Caswell, H. (1997) The relative ‘importance’ of life-history stages to population growth: prospective and retrospective analyses. *Structured-population models in marine, terrestrial, and freshwater systems* (ed. by S. Tuljapurkar and H. Caswell), pp. 247–271. Chapman & Hall, New York.
- Johnson, E.A., Miyanishi, K. & Kleb, H. (1994) The hazards of interpretation of static age structures as shown by stand reconstruction in a *Pinus contorta*–*Picea engelmannii* forest. *Journal of Ecology*, **82**, 923–931.
- Jongejans, E. & de Kroon, H. (2005) Space versus time variation in the population dynamics of three co-occurring perennial herbs. *Journal of Ecology*, **93**, 681–692.
- Keith, D.A. (1998) An evaluation and modification of World Conservation Union Red List criteria for classification of extinction risk in vascular plants. *Conservation Biology*, **12**, 1076–1090.
- Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, **142**, 911–927.
- Larson, D.W., Matthes, U., Gerrath, J.A., Larson, N.W.K., Gerrath, J.M., Nekola, J.C., Walker, G.L., Porembski, S. & Charlton, A. (2000) Evidence for the widespread occurrence of ancient forests on cliffs. *Journal of Biogeography*, **27**, 319–331.
- Lavergne, S., Thompson, J.D., Garnier, E. & Debussche, M. (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos*, **107**, 505–518.
- Lavergne, S., Thuiller, W., Molina, J. & Debussche, M. (2005) Environmental and human factors influencing rare plant local occurrence, extinction and persistence: a 115-year study in the Mediterranean region. *Journal of Biogeography*, **32**, 799–811.
- Matthies, D., Bräuer, I., Maibom, W. & Twarntke, T. (2004) Population size and the risk of local extinction: empirical evidence from rare plants. *Oikos*, **105**, 481–488.
- Médail, F. & Verlaque, R. (1997) Ecological characteristics and rarity of endemic plants from Southeast France and Corsica: implications for biodiversity conservation. *Conservation Biology*, **11**, 269–281.
- Menges, E.S. (1992) Stochastic modeling of extinction in plant populations. *Conservation biology: the theory and practice of nature conservation preservation and management* (ed. by P.L. Fiedler and S.K. Jain), pp. 253–275. Chapman & Hall, New York.
- Menges, E.S. & Dolan, R.W. (1998) Demographic viability of populations of *Silene regia* in midwestern prairies: relationships with fire management, genetic variation, geographic location, population size and isolation. *Journal of Ecology*, **86**, 63–78.
- Morris, W.F. & Doak, D.F. (2002) *Quantitative conservation biology*. Sinauer, Sunderland, Massachusetts.
- Morris, W.F. & Doak, D.F. (2005) How general are the determinants of the stochastic population growth rate across nearby sites? *Ecological Monographs*, **75**, 119–137.
- Oostermeijer, J.G.B., Brugman, M.L., Boer, E.R. & den Nijs, H.C., (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. *Journal of Ecology*, **84**, 153–166.
- Oostermeijer, J.G.B., van Veer, R. & den Nijs, J.C.M., (1994) Population structure of the rare, long-lived perennial *Gentiana pneumonanthe* in relation to vegetation and management in the Netherlands. *Journal of Applied Ecology*, **31**, 428–438.
- Petit, R.J., Hampe, A. & Cheddadi, R. (2005) Climate changes and tree phylogeography in the Mediterranean. *Taxon*, **54**, 877–885.
- Picó, F.X. & Riba, M. (2002) Regional-scale demography of *Ramonda myconi*: Remnant population dynamics in a preglacial relict species. *Plant Ecology*, **161**, 1–13.
- Quintana-Ascencio, P.F., Menges, E.S. & Weekley, C.W. (2003) A fire-explicit population viability analysis of *Hypericum*



1 *cumulicola* in Florida rosemary scrub. *Conservation Biology*,  
2 17, 433–449.  
3 Thompson, J.D. (2005) *Plant evolution in the Mediterranean*.  
4 Oxford University Press, Oxford, UK.  
5 Tuljapurkar, S.D. (1982) Population dynamics in variable

environments. III. Evolutionary dynamics of *r*-Selection.  
6 *Theoretical Population Biology*, 21, 141–165.  
7 Tuljapurkar, S.D. & Orzack, S.H. (1980) Population dynamics in  
8 variable environments I. Long-run growth rates and extinction.  
9 *Theoretical Population Biology*, 18, 314–342.

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